

OBSERVATIONS ON THE ECOLOGY OF THE PHASMATID CTENOMORPHODES
TESSULATA (GRAY).

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(Plates v-vi; two Text-figures.)

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Synopsis.

The phasmatid, *Ctenomorphodes tessulata* (Gray, 1835) is a defoliator of trees in the coastal forests of northern New South Wales where it reached outbreak proportions during 1955-56. Its known range is from Colombatti State Forest, near Kempsey, New South Wales, to Goodwood, near Maryborough, in Queensland. Outbreaks have only been recorded from forests in New South Wales. *C. tessulata* is not host specific since it has attacked a wide range of species of the genera *Eucalyptus*, *Syncarpia*, *Acacia* and *Casuarina*.

Descriptions of adults and eggs, and a key to the nymphal instars are given. The life cycle in the field, laboratory observations and experiments are described. Investigations show that cleptid egg parasites and disease of the phasmatid eggs are regulating factors.

A similar stand composition occurs in all the areas of high phasmatid population. The effect of the defoliation on the management of forests is considered.

It is suggested that the occurrence of forest fires is followed by an increase in the numbers of *C. tessulata*. The probable effect of fire on the cleptid parasites is also discussed. There appears to be a correlation between the large fires of 1951-52 and the outbreak of *C. tessulata* in 1955-56.

INTRODUCTION.

Plagues of phasmatids have been recorded on the highlands of New South Wales over the past 75 years, and although it is likely that plagues occurred prior to 1880, this is the earliest date for which accurate records are available. The species concerned in these areas are *Podacanthus wilkinsoni* Macleay, 1881, and *Didymuria violescens* (Leach, 1814). More recently *Ctenomorphodes tessulata* (Gray) has been noted in large populations on the north coast of New South Wales. It is rather surprising that these have gone unrecorded, the first indication of their presence being extensive areas of defoliated forest trees. This can be partly attributed to the great diversity of form among the Phasmatidae and their resemblance to the vegetation upon which they feed.

A recent paper by Key (1957) on kentromorphic phases in the Phasmatidae has enabled the phase patterns to be correlated with the population densities in the three species reaching plague proportions.

The taxonomy and nomenclature of this and other species has been reviewed by Key (1957), and an application has been made to the International Commission on Zoological Nomenclature for the names to be added to the official lists of generic and specific names.

The descriptions of *C. tessulata* by Gray (1835), Westwood (1859) and Bates (1865) were based on a small number of museum specimens available at that time. Bates records that collections available to him bore the data, Moreton Bay, Australia. A single specimen in the collection of the Department of Agriculture and Stock, Brisbane, Queensland, was collected at Moreton Island in 1916. Collections have been made at Byron Bay and Richmond Range State Forest in New South Wales and a small infestation was recorded from Washpool State Forest in January 1955.

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Prior to 1956, *C. tessulata* had not been recorded as a pest, but has since caused defoliation of forest trees in three widely separated areas of north-eastern New South Wales. A feature of the outbreaks was that severe defoliation occurred during 1955-56 in all three areas. Nymphs and adults which were collected in these areas exhibited the pattern of the high-density phase. Single specimens of nymphs from Wedding Bells State Forest near Woolgoolga in November 1952, and adults of the same generation collected in February 1953 were described by Key as having a low density phase pattern. No further material from this forest was studied until January 1956, when defoliation occurred over approximately 100 acres and individual small trees of *Casuarina torulosa* carried as many as thirty-six phasmatids.

High populations were recorded from Toonumbar State Forest, near Kyogle, in January 1956, when a comparatively small area of forest was defoliated. Observations were not continued in this area as a fire occurred in December 1956. Widespread, but scattered, defoliation was observed on Tanban, Ingalba and Colombatti State Forests, near Kempsey, in February 1956. Defoliation in these State Forests was negligible during the 1956-57 summer, and it appears that the population is now at a very low level.

DISTRIBUTION AND HOSTS.

Label data on specimens from several sources* have been used as a basis for establishing the known distribution of *C. tessulata*. Specimens have been collected from Colombatti State Forest near Kempsey, N.S.W., to Goodwood, near Maryborough, Queensland, but distribution is probably more extensive.

The localities from which large numbers of *C. tessulata* have been observed vary in altitude from 200 feet to 2,000 feet, while single specimens have been taken mainly in coastal areas of altitudes less than 200 feet.

Very Low Density Populations: N.S.W.: Byron Bay; Queensland: Beechmont, Beerburum, Burleigh Heads, Goodwood, Landsborough, Nerang, Petrie and Moreton Island.

Low Density Populations: N.S.W.: Washpool and Richmond Range State Forests.

High Density Populations: N.S.W.: Toonumbar, Wedding Bells, Tanban, Ingalba and Colombatti State Forests.

Specimens at the Division of Entomology, C.S.I.R.O., Canberra, were examined by Dr. K. H. L. Key, who gave their respective phase patterns. This information has been related to the observations made in various outbreak areas in New South Wales and where accurate field data are available there is a correlation between the phase pattern and the abundance of the species.

Observations on host relationships have been made in Toonumbar, Wedding Bells and Tanban State Forests, the three main outbreak areas. The nymphal stages were often found on many tree species, but only the characteristic defoliation or act of feeding was taken as establishing a positive host record. Thus many possible hosts have been rejected on the basis of inadequate evidence of attack.

Field studies establish that the following tree species† normally provide food material for *C. tessulata*: *Syncarpia laurifolia* Ten., *Eucalyptus paniculata* Sm., *E. propinqua* Deane and Maiden, *E. gummifera* (Gaertn.) Hochr., *E. maculata* Hook., *E. resinifera* Sm., *E. punctata* DC., *E. triantha* Link, *E. pilularis* Sm., *Casuarina torulosa* Ait., *Acacia floribunda* (Vent.) Willd.

Specimens were reared in the laboratory by Key (1957) on *Acacia mollissima* Willd. and *Eucalyptus dives* Schauer. Adult phasmatids, collected from Tanban State Forest during January 1957, were held at Sydney and fed on locally available material of *Angophora costata* Domin, *Eucalyptus radiata* Sieb. and *Syncarpia laurifolia*. Some

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† Identifications of trees in the field have been made by local field officers.

first instar nymphs which were collected in the field were reared entirely on *Syncarpia laurifolia* in the laboratory at Sydney.

These observations indicate that *C. tessulata* is not specific in its feeding habits as tree species of different genera, namely, *Syncarpia*, *Acacia*, *Casuarina* and *Eucalyptus*, have been attacked. It is probable that this phasmatid will feed on other species.

Other phasmatids which have occurred in high populations are more specific in their tastes, but *C. tessulata* has nevertheless exhibited selective feeding within the



Text-fig. 1.—Occurrences of *C. tessulata*.

genus *Eucalyptus*. *E. microcorys* was less preferred, for during 1956 it was observed that, while crowns of *E. microcorys* showed no defoliation which could be positively attributed to *C. tessulata*, those of *E. maculata* immediately adjacent were completely defoliated.

BIOLOGY AND DESCRIPTIONS.

During 1956 and 1957 intensive observations on *C. tessulata* were made in Tanban State Forest and in the laboratory at Sydney. Although Tanban State Forest is the southernmost of the three outbreak areas, and well separated from the others (Toowoomba and Wedding Bells State Forests), differences in the number of developmental stages of the insect between the three areas are considered unlikely to occur.

The data given hereunder, particularly in respect of the seasonal cycle, apply to material collected from Tanban State Forest. Investigations on Toowoomba or Wedding Bells State Forests have been confined to the collection of adult material and samples of litter from the forest floor.

(a) *Seasonal Cycle*: First instar nymphs were observed during late August and early September 1956, and most emergences had occurred before the end of September. Some fourth and fifth instar nymphs were collected during late September. These were always taken in areas having a north-easterly aspect, and it is presumed early hatching occurred in these situations. In general, only small variations in the proportion of the different instars were observed in the main population. The young nymphs ascended the trees near their hatching site and commenced to feed. Adults first appeared during December 1956, the males reaching maturity one or two weeks prior to the females. The adults of the high population recorded in January 1956 were not observed after February 1956, oviposition having occupied a period of 6-8 weeks.

Adults of the 1957 infestation did not survive more than a few weeks in the field, but many of those which were collected on 16th January 1957, and held in the laboratory, survived until May 1957.

(b) *Egg Studies*: Eggs were collected from forest litter during April 1956, immediately after the 1955-56 generation. Further samples were examined in December 1956 and April 1957, when it was anticipated that the 1956 hatchings had occurred. Litter samples were collected in April 1957, to assess oviposition of the 1956-57 generation. The results of these examinations are expressed in Table 1.

TABLE 1
Egg Dissections, Ctenomorphodes tessulata, Tanban State Forest.
Results expressed as percentages of total number of eggs collected.

Date of Collection.	Embryonic Development.	No Visible Development.	Parasitism.	Deterioration.	Empty Shells.
April, 1956	7.9	7.3	17.7	25.7	41.4
December, 1956 ..	0.8	2.5	7.4	34.5	54.8
April, 1957	0.0	0.0	5.8	27.0	67.2

Apparently some of the eggs laid in January and February 1956 hatched in August and September 1956, thus differing from those of *P. wilkinsoni* and *D. violescens* which usually hatch during the year following oviposition. A low percentage of eggs (2.5%) showed no development by December 1956, but these eggs appear to have deteriorated, or were parasitized later in the season. Some eggs laid by the specimens collected from Tanban State Forest in January 1957, and held at normal atmospheric conditions in Sydney, showed advanced embryonic development when examined in June 1957. Eggs of the same origin which were held in soil at 78°F. and at room temperature hatched during June and July of the same year. The embryonic period, including at least one diapause, may occupy eight months or even longer in the natural habitat. The glistening appearance which is characteristic of the freshly laid egg disappears during subsequent life of the egg when it is in soil, but no external signs such as colour changes have been noted which may indicate embryonic development.

A number of eggs from the 1956-57 generation were placed in moist soil. One batch was held at 76°F. while another was kept at room temperature and therefore subjected to diurnal variations. The latter yielded healthy first instar nymphs mainly early in the mornings (1.00 a.m.-6.00 a.m.) and only occasional hatchings took place at other times during the day. At 76°F. small and weakened first instar nymphs emerged only at irregular intervals. When transferred to plants and held at room temperature, they lived only a short time and were not observed to feed.

Once initiated the embryo develops very rapidly until it entirely occupies the chorion and it has proved difficult to obtain early developmental stages of the embryo. Of the eggs collected in April 1956, 7.7% were in an advanced stage until hatching took place in August and September 1956 (Table 1). The diurnal seasonal increase in temperatures appears to be an important stimulus to hatching, and there is evidence to suggest that the litter must be damp or wet before first instar nymphs can emerge satisfactorily.

Parthenogenesis has been recorded in the Phasmatodea by Salmon (1955) and other workers. Females of *C. tessulata* are able to produce eggs without fertilization and embryonic development and subsequent hatching occur in a proportion of these eggs.

(c) *Nymphs*: It has been determined by Key (1957) that there are six nymphal instars for the males and seven for the females. Results obtained with specimens collected at Tanban State Forest during 1956-57 agree with those obtained by Dr. K. H. L. Key working in Canberra on laboratory insects. The predominant instars collected at approximately weekly intervals are expressed in Table 2.

No overt gregariousness by the nymphs has been shown either in the field or the laboratory. The insects are most of the time in a resting state, even in dense populations. Specimens in the laboratory have been observed to feed more frequently during the day than the night, but temperature and other climatic factors probably determine times of feeding in the field. After some ecdyses the phasmatids feed on their exuviae, sometimes completely devouring them.

TABLE 2.
Tanban State Forest. Collection of Nymphs.

Date of Collection.	Predominant Instars.	Date of Collection.	Predominant Instars.
3.10.56	I and II	7.12.56	VI
26.10.56	III and IV	14.12.56	VI
2.11.56	III	21.12.56	VI
8.11.56	III and IV	28.12.56	VI, VII, A
16.11.56	IV	4. 1.57	VII, A
23.11.56	IV and V	11. 1.57	VII, A
30.11.56	VI	18. 1.57	A

(d) *Adults*: The nymphs reached maturity during the latter part of December 1956, in Tanban State Forest. First instar nymphs which had been collected from this State Forest in September 1956, and held under high density conditions at Sydney, became adults approximately one week earlier. Fifty adult males and females could be readily collected in the field during January 1957, but the insects had almost disappeared from the same area by 6th February 1957. During the previous year adults were present until the first week in March. Female specimens collected on 21st January 1957 were kept alive in the laboratory until June 1957, while males collected on the same date had all died by the end of April 1957. Adults of this species may live from 4 to 9 weeks in outbreak areas, but can be kept alive for at least five months in the Laboratory.

Observations made on Ingalba and Tanban State Forests in February 1956 and January 1957 indicate that the ratio of adult males to females is approximately 50:50, but in some sites females predominate. The ratio at emergence is not necessarily the same as that of the adults, for males become adults earlier, and they may die prior to the females.

Laboratory female specimens of *C. tessulata* laid from 300-900 eggs over a period of five months. The daily oviposition rate varied from 4 to 10 per female each day.

Copulation occurs soon after the adult stage is reached and approximately two weeks elapse before the females commence to lay. The males and females remain together for long periods and move around while feeding. Copulation occurs at irregular intervals, oviposition taking place between these acts. Neither adults, nor nymphs, exhibit any overt gregariousness.

The destructive potential of *C. tessulata* was compared with that of *P. wilkinsoni* and *D. violescens* by isolating two males in one cage and two females of the same species in another for all three species. Chewed off foliage and the faeces of these insects were collected, separated, oven-dried and weighed daily. The figures obtained were halved, to give a daily destruction rate of foliage for one specimen of each species. A

daily maximum and an average daily figure for fourteen days collection are given in Table 3.

The defaecation rates have not been interpreted statistically as insufficient material was available to design an experiment, with sufficient replications. It is apparent that *C. tessulata* is as destructive as either *P. wilkinsoni* or *D. violescens*, both in the quantity of food eaten and foliage otherwise destroyed. Extensive areas of forest have not been observed defoliated to the same extent as occurs with *P. wilkinsoni* and *D. violescens*, and this is partly explained by the adults of *C. tessulata* being comparatively short-lived in the outbreak areas. Phasmatids of the highlands are in the adult stage for approximately three months, while *C. tessulata* has not been observed six to eight weeks after maturity.

TABLE 3.
Comparison of Destructive Potential of Three Plague Phasmatids.
Results shown as grammes of oven-dry weight of material per insect per day.

Phasmatid.	Faeces.	Foliage.	Total.
<i>P. wilkinsoni</i> (male)			
Maximum	0.092	0.092	0.184
Average	0.054	0.044	0.098
<i>P. wilkinsoni</i> (female)			
Maximum	0.296	0.131	0.427
Average	0.188	0.066	0.254
<i>D. violescens</i> (male)			
Maximum	0.140	0.140	0.280
Average	0.084	0.023	0.107
<i>D. violescens</i> (female)			
Maximum	0.211	0.196	0.407
Average	0.156	0.062	0.218
<i>C. tessulata</i> (male)			
Maximum (1 day) ..	0.012	—	0.012
Average (1 day) ..	0.012	—	0.012
<i>C. tessulata</i> (female)			
Maximum	0.278	0.337	0.615
Average	0.176	0.111	0.287

It has been possible, in the case of the three plague phasmatids studied by Dr. K. H. L. Key, to correlate the high density phase pattern with most field outbreaks. This should enable entomologists to approximate the density of a population from which one or two specimens have been collected from the field. Large populations of immature phasmatids during the last ten years have not always been recorded until defoliation has become apparent in spite of the fact that single specimens have been collected and sent to entomologists for examination. Now, in the light of present knowledge, when nymphs show the medium to high density phase pattern, the population may warrant further investigation.

The following descriptions which are intended for use in the field will serve to distinguish *C. tessulata* from the other two species of injurious Australian phasmatids. They are based on fourteen males and twenty-three females in the collection of the Forestry Commission of New South Wales.

Male (Plate v, fig 1): Head bearing two large compound eyes and three ocelli. Antennae 26-segmented. Pronotum approximately 3 mm. long, surface uneven, narrower than head. Mesonotum approximately 13 mm. long, two rows of prominent dorsal tubercles numbering in all from 8 to 13, several slightly raised lateral tubercles, narrower than the pronotum. Metanotum approximately 7 mm. long, without tubercles, wider than mesonotum. Prothoracic legs bearing no spines, femora of mesothoracic legs carry spines along their length with two large spines at distal end. Spines evident along femora and tibiae of metathoracic legs and distal end of each. Tegmina brown, approximately 10 mm. long. Hindwings approximately 35 to 40 mm. long extend over fifth and sometimes part of sixth abdominal segments. Ten abdominal segments.

Genital lobes appear as enlargement on ventral surface of segments VIII and IX. Tenth segment modified to form claspers which bear spines. Cerci about $\frac{1}{3}$ inch long, leaf-like.

Female (Plate v, fig 2): Head bearing two large compound eyes and three ocelli. Antennae 25-28-segmented, shorter than those of male. Pronotum approximately 5 to 7 mm. long, no tubercles present, slightly narrower than head. Mesonotum 20 to 23 mm. long with two rows of dorsal tubercles and several lateral tubercles. Tubercles more prominently raised than in male. Metanotum 7 to 8 mm. long, non-tuberculate. Pronotum, mesonotum and metanotum of equal width. Prothoracic legs bearing spines along, and at distal end of femora. Mesothoracic legs with spines along femora and tibiae, as well as at distal end of these segments. Spines also present along and at distal extremities of femora and tibiae of metathoracic legs. Tegmina brown, approximately 13-15 mm. long. Hindwings 25 to 30 mm. long, apices extending almost to posterior margin of third abdominal segment. Ten abdominal segments. Operculum which covers genital valves arises from segment VIII, its apex extending beyond segment X and located between the cerci. Cerci about $\frac{1}{4}$ inch long, leaf-like.

General colour of the males and females light to dark brown.

The Egg: In the Phasmatoidea the egg may be regarded as a useful taxonomic accessory. Egg approximately 3 mm. long and 2 mm. in diameter at broadest point. Roughly elliptical in shape, somewhat wider in region of micropyle, distinctly flattened at both ends. When freshly laid, glistening black in appearance. Pale grey area extending over and around micropylar area. Smooth edged grey pigment appearing to overlie the black. Egg smooth, although microscopic examination shows it to be uneven. Black raised ridge in the shape of a Y surrounds the micropylar orifice at non-opercular end of egg.

Key to the Instars of C. tessulata.

Sex determination:

1. Operculum or minute furrow* on abdominal sternum VIII present female.
2. Operculum or minute furrow on abdominal sternum VIII absent male.

Male.

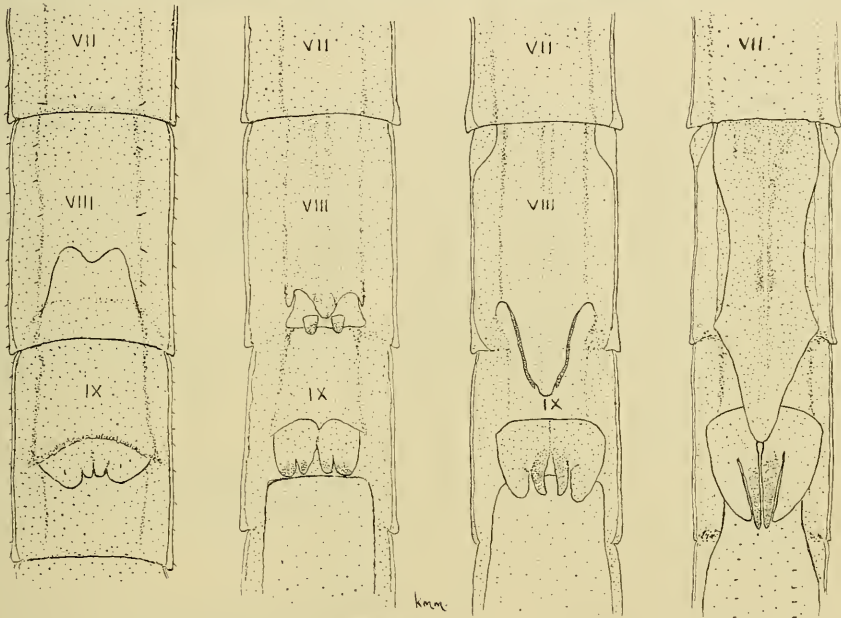
1. Lateral and dorsal mesothoracic tubercles not raised: wing rudiments not evident; antenna with 9 segments which are clearly separated, length approx. 12 mm. INSTAR 1.
Lateral and dorsal tubercles raised 2.
2. Dorsal tubercles not black: wing rudiments evident; antenna with 9 segments, several partially divided; length approx. 20 mm. INSTAR 2.
Dorsal tubercles black 3.
3. Apices of tegmen rudiments not extending over the metanotum: wing rudiments not in contact along their inner margin; antenna with about 18 distinct or partially divided segments; length approx. 30 mm. INSTAR 3.
Apices of tegmen rudiments extending over the metanotum 4.
4. Wing rudiments not in contact along their inner margins: antenna with about 19 distinct or partially divided segments; length approx. 40 mm. INSTAR 4.
Wing rudiments in contact along their inner margins 5.
5. Wing rudiments not extending to the posterior margin of abdominal segment 1: apices of tegmen rudiments do not reach the anterior margin of wing rudiments; antenna with about 22 segments; length approx. 55 mm. INSTAR 5.
Wing rudiments extending beyond the posterior margin of abdominal segment 1; apices of tegmen rudiments almost reaching the anterior margin of wing rudiments; antenna with about 24 segments; length approx. 70 mm. INSTAR 6.

Female.

1. Lateral and dorsal mesothoracic tubercles not raised: wing rudiments not evident; operculum present as a transverse furrow on sternum VIII; antenna with 9 distinct segments; length approx. 12 mm. INSTAR 1.
Lateral and dorsal mesothoracic tubercles raised 2.
2. Dorsal tubercles not black: operculum present as a pointed triangular projection on sternum VIII, Text-fig. 2; antenna with 9 segments, several of which are partially divided; length approx. 20 mm. INSTAR 2.
Dorsal tubercles black 3.

* Minute transverse furrow is present only in Instar 1, and live or recently killed material is necessary to see this structure.

3. Operculum not covering anterior genital valves on sternum VIII, Text-fig. 2; wing rudiments minute; antenna with about 18 distinct or partially divided segments; length approx. 30 mm. INSTAR 3.
Operculum covering or almost covering anterior genital valves on sternum VIII, Text-fig. 2 4.
4. Tegmen rudiments extending not more than half their length over anterior margin of metanotum; antenna with about 19 distinct or partially divided segments; length approx. 45 mm. INSTAR 4.
Tegmen rudiments extending more than half their length over anterior margin of metanotum 5.
5. Apex of operculum extending half-way along sternum IX, Text-fig. 2; and partly covering posterior genital valves; wing rudiments not in contact along their inner margins; tegmen rudiments separated along inner margin; antenna with about 22 segments; length approx. 55 mm. INSTAR 5.
Apex of operculum extending more than half-way along sternum IX 6.



Text-fig. 2.—Nymphal characteristics. From left: abdominal sterna of female instars.

6. Inner margins of wing rudiments not touching: operculum reaching posterior margin of segment IX, or almost reaching apices of posterior genital valve; wing rudiments extending almost to base of metacoxae. Tegmen rudiments extending at least half their length beyond anterior margin of metanotum; antenna with about 24 segments; length approx. 75 mm. INSTAR 6.
Inner margins of wing rudiments touch; operculum reaching to or beyond midpoint of segment X and exceeding apices of posterior genital valve; wing rudiments strongly tessellated, extending to base of metacoxae; apices of tegmen rudiments almost reaching anterior margin of wing rudiments. Antenna with about 26 segments; length approx. 110 mm. INSTAR 7.

MORTALITY FACTORS.

Several factors have caused, or have been suspected of causing, mortalities in the various stages of *C. tessulata*.

(a) *Temperature and Moisture*: The effects of weather in the field have not been studied, all observations being made on insects in the laboratory. Nymphs were at first difficult to rear, but when water was sprayed onto the leaves, the first instar phasmatids were observed to consume some of it and mortalities were reduced. When nymphs were held in jars with an adequate supply of food they were reared through

successive instars. A more successful method consisted of placing the recently hatched nymphs on young plants in nursery tubes, which were placed in a small container of moist soil, within a wire gauze cage approximately 24 in. × 18 in. × 18 in. The foliage was sprayed with water at least twice a day and the soil was watered on alternate days. Mortalities were low and nymphs were observed to feed during the third day. Key (1957) successfully reared the phasmatids from first instar nymphs by placing them in small wire mesh cages which were located over a container of water holding the leaves and covered with an inverted, loosely fitting plastic jar. An atomizer was used to spray the foliage twice a day during the early instars, and once a day during later instars.

Recently emerged nymphs apparently require moist conditions, which would be supplied as rain and dew in the field. Most emergences from eggs in the laboratory occurred during the early hours of the morning and their moisture requirements would probably be fulfilled by condensation. Moisture is apparently less critical during the later instars and in the adult stage, but prolonged dry conditions, particularly if accompanied by moderate to high temperatures, could cause high mortalities among the early instars.

First instar nymphs obtained from eggs held at 76°F. died a few days after being placed on food at temperatures of 55°F. to 65°F., but nymphs which hatched at temperatures of 55°F. to 65°F. and were placed with those hatched at 76°F. were reared successfully. Eggs held exposed under laboratory conditions of atmospheric humidity and temperature failed to hatch, while those kept in moist soil hatched normally. However, lack of moisture did not inhibit embryonic development, so that under dry conditions high mortalities would occur at hatching. Conditions such as these would not occur frequently under field conditions.

(b) *Food*: This species has been reared on *Syncarpia laurifolia*, *Acacia mollissima* and *Eucalyptus dives*, and a large percentage of the nymphs were reared to adults when any one of these host plants was used exclusively. In the field, recently emerged nymphs which ascend a tree, the foliage of which is not acceptable to them, may desiccate before a suitable host species is found.

(c) *Previous History of the Eggs*: Some eggs which were obtained from the 1955-56 generation showed no hatching although exposed to conditions which apparently stimulated hatching of the eggs obtained from the 1956-57 generation. Such factors as food requirements of the mature female, parthenogenesis and others which have not been elucidated, may affect the viability of the eggs.

(d) *Cannibalism*: Key (1957) records cannibalism as a possible mortality factor, and he states that chewed legs of recently moulted nymphs have been found in the rearing cages. When rearing specimens at Sydney, no cannibalism was noticed, but when ecdysis was completed, freshly emerged nymphs were observed to consume their exuviae and frequently the exuviae of others. This has been observed before ecdysis was completed; thus a nymph which has not shed the exuviae from its legs may possibly have them chewed off by another nymph. This could account, to some extent, for instances of limb regeneration frequently encountered in this species. Cannibalism is not considered to be a mortality factor of laboratory or field specimens, even though most mortalities of nymphs in the laboratory occurred at ecdysis.

(e) *Fire*: A large forest fire could be catastrophic to phasmatid populations, and it may destroy many insects and reduce their available food supply. A limited fire occurred on Toonumbar State Forest in December 1956, and insects which had emerged during the August or September may have been killed. This has been confirmed by observations since the fire.

(f) *Disease*: During mortality studies of *Podacanthus wilkinsoni*, Casimir and Edwards (1955—unpublished report, Forestry Commission N.S.W.) isolated a species of entomogenous fungus from nymphs and adults, but they state that this does not present sufficient evidence of pathogenicity. No instances of death attributable to pathogens have been determined, nor has it been possible to relate micro-organism activity with mortalities of *C. tessulata*. Nymphs have died when held at high humidities in the

laboratory and, some time after death, a fungal growth spread over the surface of their bodies. This fungus was considered to be a saprophytic type.

Dissections of eggs collected from the north coast outbreak areas showed a high mortality percentage from diseases of unknown origin (Table 1). Deterioration due to fungi, bacteria and physiological causes about which little is known at present has affected 25.7%, 34.5% and 27.0% of total eggs collected in April 1956, December 1956 and April 1957, respectively. From eggs of *C. tessulata* which showed deterioration, two fungi, *Verticillium* sp. and *Penicillium* sp.,* have been isolated. Both are commonly found in the soil and it is unlikely that they would be the primary cause of the deterioration.

(g) *Predators*: Insect predators have not been recorded attacking any stages of *C. tessulata*, although such attacks probably occur. Nymphs of the highland plague species have been attacked by *Harpobittacus* sp.† (Bittacidae-Mecoptera) in the Jenolan area.

Birds feed on phasmatids, but observations only include crows feeding on *D. violescens* and *P. wilkinsoni* in the highland areas. No doubt *C. tessulata* also falls prey to birds, although no instance of this has been observed. The resemblance of phasmatid eggs to seeds is rather striking, as can be seen from Plate vi.

Eggs of *C. tessulata* are shiny black and when freshly laid are easily discernible in the forest litter, but when the eggs lose their lustre, they become difficult to locate, as soil adheres to their surface. Quail have been active in Tanban State Forest during the latter part of the outbreak, and it is possible that there is some association between the activity of these birds and the reduction in the number of eggs.

(h) *Parasites*: Egg parasites of the genus *Myrmecomimesis* (Cleptidae-Chrysoidea) have been described by Riek (1955). The material examined by him was mainly obtained from the Jenolan area where plagues of *Didymuria violescens* and *Podacanthus wilkinsoni* were present. Eggs of *D. violescens* from Bago State Forest have yielded a total parasitism of up to 9% during 1954-55. During 1952, parasitism of *P. wilkinsoni* eggs averaged as much as 7% from several collecting sites on the Jenolan area.

The males of the several species of *Myrmecomimesis* found on the coast are winged while the females are wingless. Parasitized phasmatid eggs can be distinguished by the presence of small pits on the surface of the chorion, made by the female wasp when ovipositing. A small hole passes from at least one of these pits, through the vitelline membrane, causing the latter to become dark brown at the puncture. One egg may show several of these punctures, but only one parasite develops in each egg. Whether the pits are the result of exploratory efforts by the adult parasite in determining a suitable oviposition site or whether several parasites have actually oviposited in the egg has not been determined.

Phasmatid eggs which were laid during January and February 1956 were found to contain parasites when examined in April 1956. The parasite larva completely occupied the vitelline membrane indicating that development to this stage was comparatively rapid. The eggs were held in the laboratory until December 1956, when adult cleptid wasps emerged. Diapause may occur since the larvae remain in an advanced larval stage until November or December, although the phasmatid eggs are parasitized during January to April of the same year.

Attempts to induce parasitism by exposing *C. tessulata* eggs to *M. rubrifemur* under confined conditions were unsuccessful and a detailed study on the life cycle of *Myrmecomimesis* spp has not been made.

The specimens of *Loboscelidea* sp.‡ were obtained shortly after eggs and forest litter were received from Tanban State Forest in April 1956. No emergences occurred later

* Specimens examined by D. W. Edwards, Pathologist, Forestry Commission, N.S.W.

† Observations by L. Mors, Forester, Oberon, 1955.

‡ This species is being described by Mr. E. F. Riek, Division of Entomology, C.S.I.R.O., Canberra.

in the year, as was the case with *Myrmecomimesis* spp. This indicates that certain differences exist between the life cycles of the two parasites. Since *Myrmecomimesis* sp. is more abundant than *Loboscelidea* sp., it is probable that the former would account for more parasitism.

Parasitism of *C. tessulata* eggs from the coast is given in Table 4. In addition, fluctuations in parasite numbers have been recorded for Tanban State Forest and these

TABLE 4.
Egg Dissection of April, 1956, Collection.
Expressed as percentages of total eggs collected.

State Forest.	Embryonic Development.	No Development.	Parasitism.	Deteriorated.	Empty Shells.
Toonumbar ..	19.4	13.2	20.6	21.4	25.4
Wedding Bells ..	2.0	1.9	12.4	21.2	62.5
Tanban	7.9	7.3	17.7	25.7	41.4
Ingalba	15.9	16.4	20.0	24.0	23.7
Colombatti ..	5.6	8.1	7.5	48.2	30.6

are expressed in Table 1. Parasitism of *C. tessulata* eggs is greater than that of either *P. wilkinsoni* or *D. violescens* in the highlands, and this has been verified by observations on the forest litter in Tanban State Forest in February 1956, when the parasites were active. At no time have the parasites been observed to be so abundant in the highland areas as to be apparent in the litter. The parasite which has occurred in all outbreak areas and in greatest abundance is *Myrmecomimesis rubrifemur* (Riek). The known occurrences of the other species are given in Table 5, but more extensive collections would probably have given a greater distribution of the species involved.

TABLE 5.
Occurrence of Cleptid* Parasites in Outbreak Areas.

Location.	Species.
Toonumbar State Forest	<i>Myrmecomimesis rubrifemur</i> (Riek).
Wedding Bells State Forest	<i>M. rubrifemur</i> (Riek).
Tanban State Forest	<i>M. rubrifemur</i> (Riek). <i>M. nigripedice</i> (Riek). <i>Loboscelidea</i> sp.
Ingalba State Forest	<i>M. rubrifemur</i> (Riek). <i>M. nigripedice</i> (Riek). <i>M. bispinosa</i> var. (Riek).

* Determinations by E. F. Riek, Division of Entomology, C.S.I.R.O., Canberra.

DISCUSSION.

(a) Effect of Outbreaks on the Stand Composition and Forest Management.

The tree stand composition in all areas attacked by *C. tessulata* shows considerable similarity. Attack appears to be restricted to some of the drier type coastal hardwood forests of northern New South Wales.

A typical stand in which the attack occurs consists of *Eucalyptus punctata* (Grey Gum), *E. triantha* (White Mahogany), *E. paniculata* (Ironbark), *E. maculata* (Spotted Gum), *E. gummifera* (Red Bloodwood), *Syncarpia laurifolia* (Turpentine) and Stringybark. Always associated with attacked stands is an understory of *Casuarina torulosa* (Forest Oak), and *E. microcorys* (Tallowwood) is often associated with them. Other species which are occasionally found in attacked areas are *E. resinifera* (Red Mahogany), *E. umbellata* (Gaertn.) Domin (Red Gum), *E. saligna* (Blue Gum), *Tristania conferta*, R. Br. (Brush Box) and *Angophora* spp. (Wild Apple). The understory, particularly in the Kempsey area, consists mainly of Leguminosae. On Tanban State Forest, in the Kempsey district, phasmatids have attacked a stand of *E. pilularis* (Blackbutt), this

being associated with Grey Gum, Spotted Gum, White Mahogany, Ironbark, Stringybark and Turpentine. *E. pilularis* constituted more than 50% of the stand, and this is the only instance recorded where *C. tessulata* has attacked this species.

As *C. tessulata* has avoided *E. microcorys* in preference to other species of eucalypts, it was thought that this selectivity may have been accounted for on the basis of oil content of the leaves. A chemical examination of the leaves of favoured hosts and those of *E. microcorys* showed that the major oil constituents were very similar, and from these analyses both types of leaves should be equally acceptable. The minor constituents of the oils were not determined, and it is possible that these may account for the observed selectivity in the feeding habits.

Attack by *C. tessulata* in plague proportions has not yet been recorded as recurrent. The plagues during 1955-56 severely or completely defoliated areas of up to 100 acres. In 1956-57 the phasmatid population was less, and by the mid-summer of 1956-57 all of the trees attacked the previous season had recovered and recognition of the areas which had been severely affected the previous year was difficult. Severe attack on isolated areas without further heavy infestations the following season would be unlikely to have any serious or lasting effect on the trees, while repeated defoliations would either kill or retard the growth of the preferred species, and Tallowwood may be favoured as against the more susceptible species. The removal of cover would enable a greater degree of light to penetrate to the forest floor, thus releasing suppressed lignotubers. This again would be likely to favour the development of tallowwood stands rather than the more susceptible species.

The attacked stands contain only a small proportion of Tallowwood and it would be some time before it regenerated sufficiently to restock an area, particularly as the outbreak areas are of low site quality. When considering the merits of restocking with Tallowwood, it should be remembered that *C. tessulata* attacks many other valuable species.

(b) Influence of Forest Fires.

In 1951-52, fires burnt over large tracts of forest on the north coast, including those areas where outbreaks of *C. tessulata* were later to occur. The same areas were sometimes burnt more than once during the same season, particularly on Tanban State Forest. Although data have been available on the extent, intensity and date of occurrence of the fires, it was realized that the actual boundaries of the affected areas would be only approximate. For this reason the fire records have been related to phasmatid outbreaks only in a general manner.

Fires were recorded from Tanban, Ingalba and Colombatti State Forests and adjoining private property between 26th August 1951 and 4th January 1952, but in the six years since that time no extensive burns have occurred. Observations during the phasmatid plague of 1955-56 revealed that high populations were restricted to definite areas, whilst a low-density population existed throughout the rest of the regions. These high populations have occurred in most instances close to or within the limits of areas burnt in 1951-52.

Records of fires on Wedding Bells State Forest show that areas heavily infested by phasmatids in 1955-56 were burnt in 1951-52 during the period from 30th September to 26th October 1951, and local observations confirm these records. The phasmatid infestation of 1955-56 in Toonumbar State Forest was found to be present on a site which had not been burnt for at least eight years. A widespread fire did occur on 23rd September 1951, but this was some distance from the outbreak area. These fires varied in intensity from light ground fires to crown fires, and within a comparatively small area damage would have been caused to the crown of some trees whilst those in close proximity remained relatively untouched. The leaf litter is destroyed only by the hotter burns.

Nymphs of *C. tessulata* emerge in late August and early September when they ascend the trees, usually to the more tender terminal shoots. The egg parasites appear

to emerge mainly during December and February, when the eggs of *C. tessulata* are available for parasitism.

Fires which occur in the spring and early summer months may destroy the parasitized eggs of *C. tessulata* on the forest floor, and if the fire were not intense, it is likely that the developing nymphs present in the crowns of the trees would be unaffected. The eggs from this generation hatch the following spring; thus an increase in population could occur over the succeeding years. The figures of parasitism in Table 1 indicate that the cleptid parasites are important mortality factors and their destruction would remove their regulating influence on the phasmatid population, with a consequent rise in phasmatid numbers.

Records of fires on Ingalba, Tanban, Colombatti and Wedding Bells State Forests appear to be related to phasmatid plagues, although there are some areas in these State Forests which have been attacked by phasmatids without having been affected by fire.

The nymphal and mature phasmatids of the 1956-57 season disappeared prematurely from the outbreak areas, and this cannot be attributed to the activity of cleptid egg parasites which had greatly increased in number during the absence of fires. This points to the fact that at least one other major regulating factor, at present undetermined, was operating during the 1956-57 season. Climatic records for January and February 1957 do not suggest climate as the main factor, for adult phasmatids held in cages at Sydney lived many months. No dead phasmatids were collected from the forest litter, nor were any observed to exhibit moribund symptoms which may indicate disease.

Females of *C. tessulata* are flightless, and migration could not account for the decrease in population.

While fires may have had an influence by temporarily reducing the egg parasite population, it is also suggested that fires either in or near plague areas have had their influence on the bird population. This may have resulted in an increase in the population of *C. tessulata*, by the regulating factors being partly removed. The occurrence of a univoltine life cycle and the high egg laying potential of *C. tessulata* have probably enabled plagues to occur within four years of the fires.

After a period of five years high populations of *C. tessulata* are no longer present and it appears that there has been a return to a more stable environment. It will not be easy to test the hypothesis of predatism by birds without high populations of *C. tessulata*. As the practice of burning the litter on the forest floor in the spring and summer period may prolong phasmatid plagues by destroying the egg parasites, the relative merits of controlled burning should be considered in relation to plagues of *C. tessulata*. The effects of fires on the environment of a forest are not always fully realized.

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References.

- BATES, H. W., 1865.—*Trans. Linn. Soc. London*, 25: 347.
 CRAIGHEAD, F. C., 1950.—Insect enemies of eastern forests. *U.S.D.A. Misc. Publ.* No. 657, p. 97.
 EATON, C. B., 1952.—Walkingstick damage in hardwood stands and its control with D.D.T. aerial sprays. *Progr. Rep. For. Insect Lab. Milwaukee, Wis.*, April.

- GRAY, G. R., 1835.—*Synopsis of the species of insects belonging to the family of Phasmidae*, 44 pp. (London).
- KEY, K. H. L., 1957.—Kentromorphic phases in three species of Phasmatodea. *Aust. J. Zool.*, 5 (3): 247-284.
- O'CONNOR, B. A., 1949.—Some insect pests of Tonga. *Agric. J. Fiji*, 20 (2).
- RIEK, E. F., 1955.—Australian Cleptid (Hymenoptera Chrysoidea) egg parasites of Cresmododea (Phasmodea). *Aust. J. Zool.*, 3 (1): 118-130.
- SALMON, J. T., 1955.—*Tuatara*, 5 (3): 77-81.
- WESTWOOD, J. O., 1859.—*Cat. Phas. Brit. Mus.*, p. 115.

EXPLANATION OF PLATES V-VI.

Plate v.

1. *Ctenomorphodes tessulata*. Adult male.
2. *Ctenomorphodes tessulata*. Adult female.
3. *Myrmecomimesis* sp. A parasite of Phasmatid eggs.
4. An outbreak area. Tanban State Forest, February, 1957. *E. maculata* with understorey of *C. torulosa*.

Plate vi.

Phasmatid eggs. Top row, left to right: *Ctenomorphodes tessulata* (Gray), *Ctenomorpha chronus* (Gray), *Podacanthus wilkinsoni* Macleay, *Podacanthus viridiroseus* (Gray), *Podacanthus typhon* Gray. Bottom row, left to right: *Didymuria violescens* (Leach), *Acrophylla titan* (Macleay), *Ertatosoma tiaratum* (Macleay), *Tropidoderus childreni* (Gray).